

MORPHOLOGY AND PHYTOGEOGRAPHY: THE CLASSICAL APPROACH TO THE STUDY OF DISJUNCTIONS

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Disjunctions are evident in the distribution of almost every species of plant, for it is obvious that no species is composed of completely continuous populations. Discontinuities, however, range from small to very large. Although formerly widely distributed, the giant redwoods or big trees (*Sequoiadendron giganteum*) now occur in groves (populations) of varying size scattered over a distance of 250 miles along the western slopes of the Sierra Nevada of California. The gaps between groves may be insignificant or up to 50 miles wide, but disjunctions of this size do not draw particular attention, except as showing that the intervening habitats presumably are now unfavorable for the establishment and growth of *Sequoiadendron*. If, however, a grove of big trees were to be found in some part of the world as remote from California as the Himalayas of Nepal or the Smoky Mountains of North Carolina and Tennessee, the find might be more exciting than the discovery of living *Metasequoia* in central China. To the inquisitive mind such a large gap in distribution would demand explanation, and, unsurprisingly, disjunctions of this size are the ones that have most intrigued biologists.

A disjunction in the distribution of a single species or genus, even a very wide one as in the hypothetical example above, may make one wonder, but when numerous species in the flora of a given region show the same general disjunction, the curious scientist who realizes that there is a common pattern can hardly resist searching for the circumstances behind it. Patterns of disjunction between eastern North America and eastern Asia, between Europe and North America, between eastern and western North America, and between North and South America are among those that have proved to be especially intriguing (at least to biologists of the continents involved). Almost from Linnaeus onward, botanists have sought and advanced explanations as diverse as double creation of species, long-distance dispersal, disruption (by a variety of factors) of formerly continuous ranges, drifting of continents, and the either conscious or unintentional activities of man.

A great deal of effort has gone into the study of disjunct distributions, and in all of the published material that has resulted, it is evident that comparative morphology is basic. Morphology is basic to the study of disjunctions (and to all of phytogeography, for that matter), because it is basic to taxonomy. Without a taxonomic frame of reference for each disjunct taxon comparisons of almost any sort become meaningless. As taxonomic ideas about a taxon change, so must conclusions based upon the earlier taxonomy. The new data brought into taxonomy by biosystematics have not upset the fundamental taxonomic framework built on morphology but have generally confirmed its soundness. The new data have, moreover, served to broaden the parameters of taxonomy, at the same time

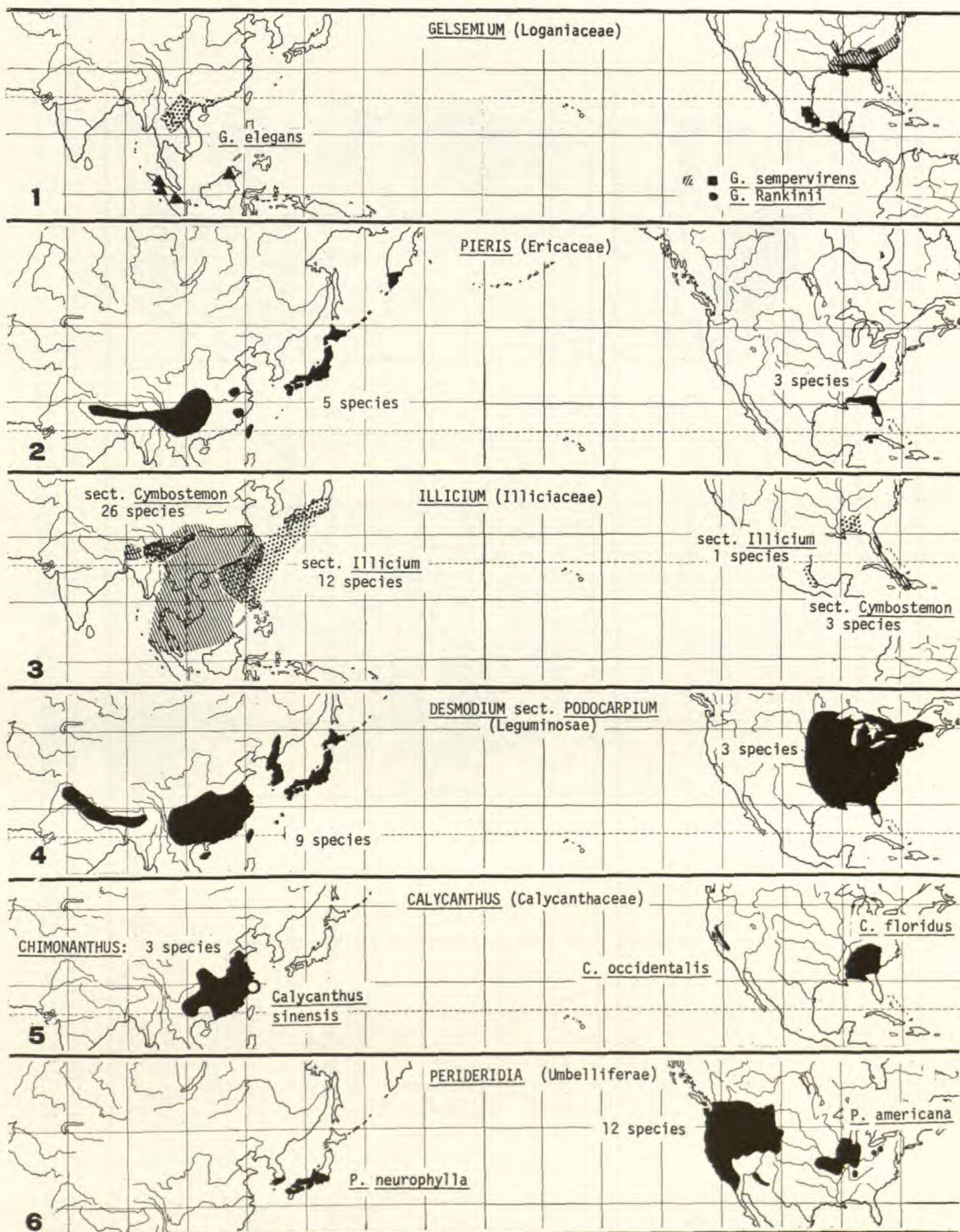
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strengthening its framework and providing new clues that help to untangle knotty evolutionary problems. Similarly, in the study of disjunctions new techniques are providing new clues that comparative morphology alone cannot. Modern botanists are using data from geology, palaeobotany, ecology, palynology, cytology, genetics, physiology, and chemistry in their search for further evidence that will help to explain the fascinating patterns of disjunction in the distribution of plants.

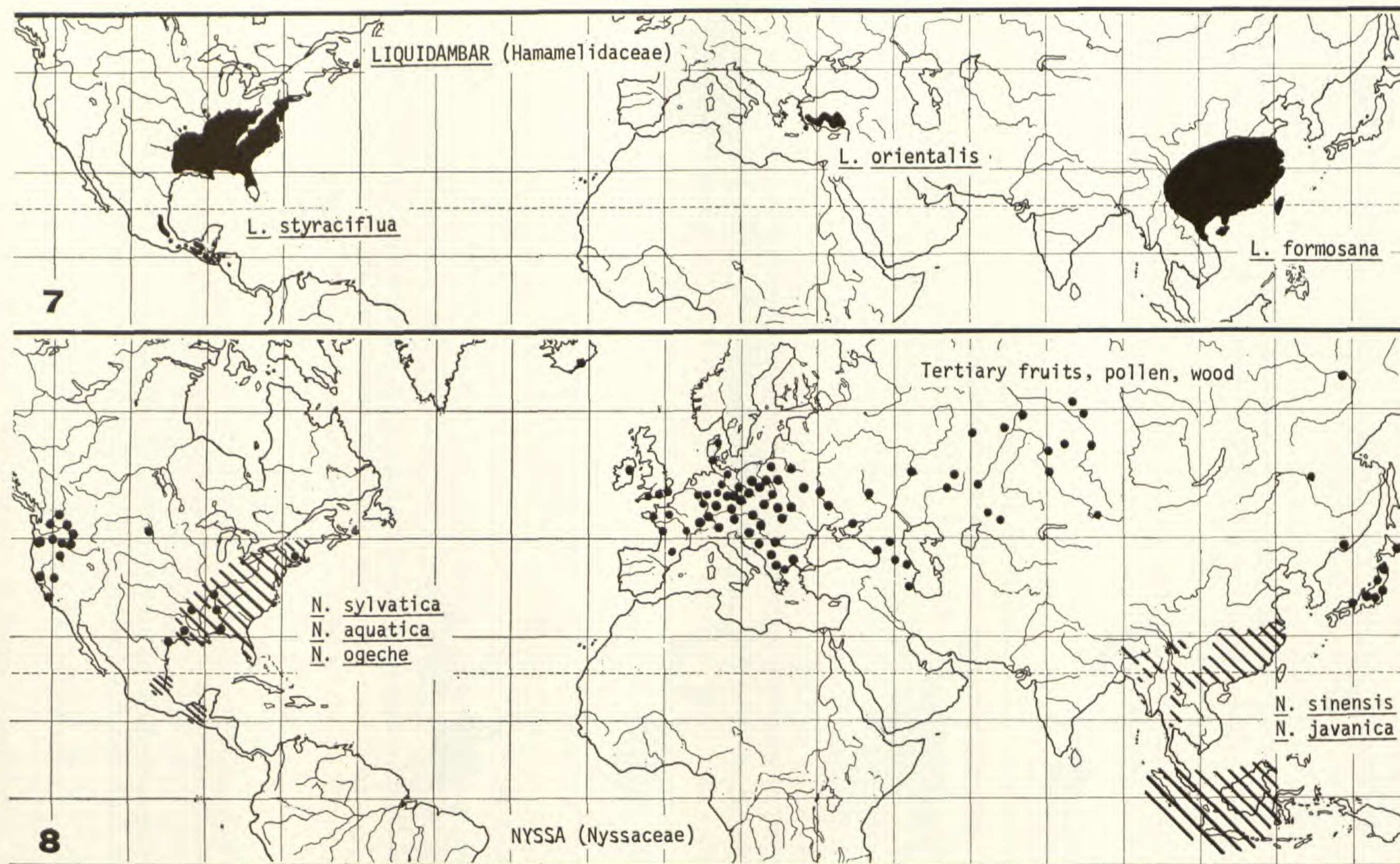
Before considering various aspects of morphology and taxonomy involved in the study of disjunctions in the ranges of plants, it may be useful to look more or less briefly at three of the patterns of disjunction in the distribution of North American plants: Tertiary relict disjunctions; eastern North American–western North American disjunctions; and North American–South American disjunctions.

Tertiary Relict Disjunctions (Maps 1–11).—This pattern of disjunction is an extension of the spectacular and long-known eastern North American–eastern Asian floristic relationship (Maps 1–3, 8) that was first commented on by Linnaeus (1750; *cf.* Graham, 1966), later recognized independently by Thunberg (1784) and Castiglioni (1790; *cf.* Li, 1955), but really brought to the attention of American and European scientists by Asa Gray through a series of papers published between 1840 and 1878 (Gray, 1840–1878). In the most important paper of the series Gray (1859) showed that there are numerous similarities between the floras of eastern North America and Japan, similarities so marked in many instances that it appeared to him that the same species occurred in both regions. Surprisingly, similarities between the floras of Japan and western North America were fewer, and many of the “identical species” common to the eastern parts of both continents were missing. To explain the presence of the same species in both Japan and eastern America Gray advanced an hypothesis involving migration and interchange of species of Asia and America across the region of the Bering Strait followed by disruption of the continuous ranges by the Pleistocene glaciations, ideas that have played a fundamental role in the development of plant geography. Subsequent discoveries, especially in China, have revealed even stronger floristic ties between eastern and southeastern Asia and eastern North America. At present, the two areas are known to share at least seven pairs of closely related genera, 62 genera that now occur nowhere else, and at least 24 more widely distributed genera that have closely related species or groups of species in the two regions (Maps 1–4, 8). It has also become evident that most of Gray’s (1859) original “identical species” are morphologically distinguishable in the two areas, and, in most instances, are quite distinct (*cf.* Li, 1952), with the exception of circum-boreal species and a few others. There seem to be only relatively few identical species that are disjunct between the two areas (*e.g.* *Tipularia discolor*, *Cypripedium arietinum*, both of which may possibly be examples of long-distance dispersal, and *Alnus maritima* [*A. japonica*] with its truly amazing disjunctions between Asia, Oklahoma, and Delaware), although there are a number of species that are treated by various authors as distinct at the varietal, subspecific, or specific level (*e.g.* *Adlumia fungosa*, *Penthorum sedoides*, *Gaultheria hispidula*, *Phryma leptostachya*).

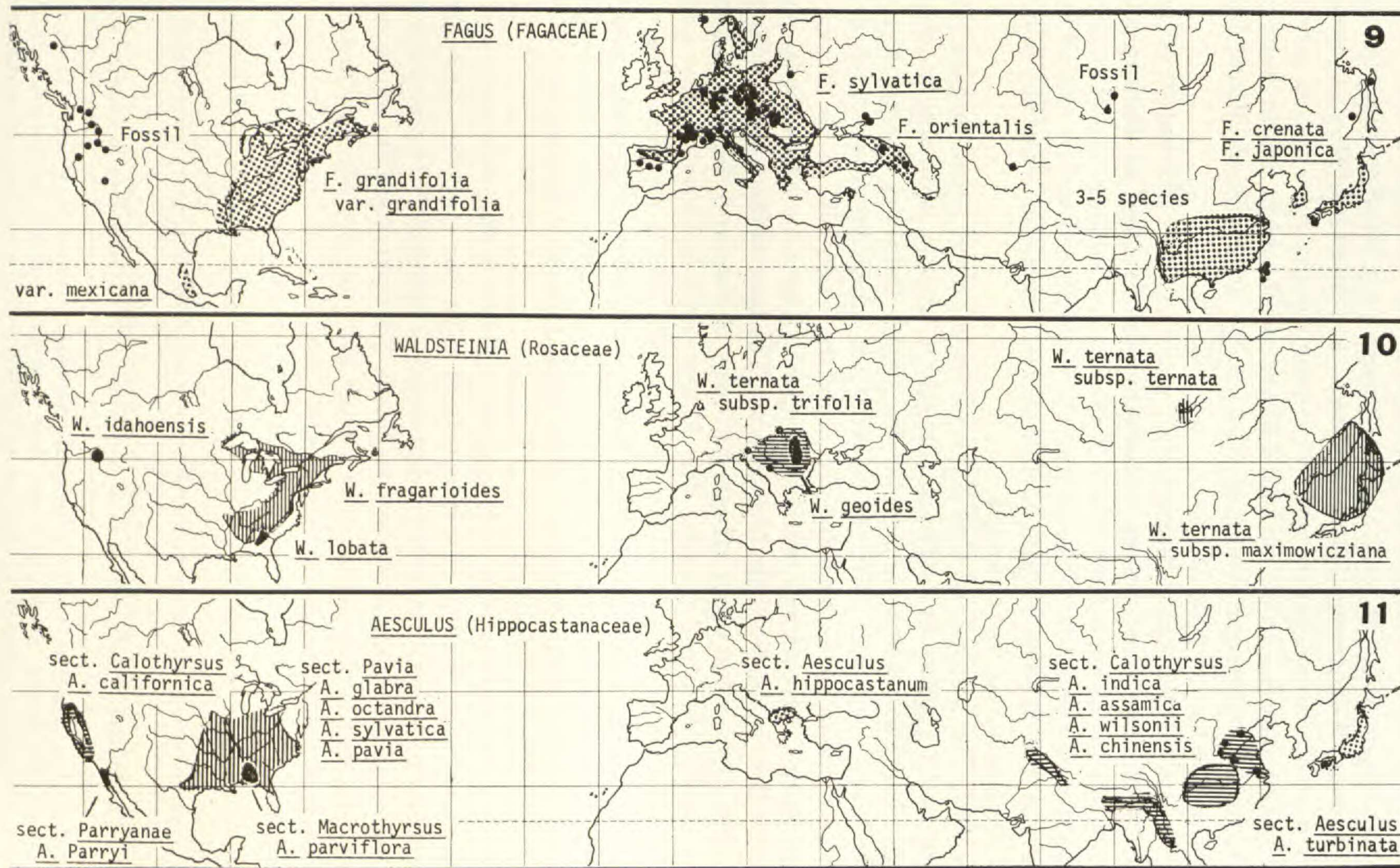
Beyond this bicentric distribution there are also at least ten genera that have



MAPS 1-6.—1-4. Some taxa restricted to eastern Asia and eastern North America.—1. *Gelsemium* (after Ornduff, 1970).—2. *Pieris*.—3. *Illicium* (after Smith, 1947).—4. *Desmodium* section *Podocarpium* (after Isley, 1951).—5-6. Two examples of taxa restricted to eastern Asia, western North America, and eastern North America.—5. *Calycanthus* (largely after Nicely, 1965).—6. *Perideridia* (after Chuang & Constance, 1969).



MAPS 7-8. Two relict Tertiary genera.—7. Extant species of *Liquidambar* (courtesy of A. L. Bogle; *L. styraciflua* after Little, 1971).—8. *Nyssa*, hatched areas, extant species; dots, Tertiary occurrences (after Eyde, 1963, and Eyde & Barghoorn, 1963).



MAPS 9-11. Three genera with relict Tertiary distribution.—9. *Fagus*, stipples, extant species; dots, records from Tertiary deposits (after Tralau, 1962; Little, 1971).—10. Extant species of *Waldsteinia* (after Teppner, 1968).—11. Extant species of *Aesculus*, note distribution of sections *Aesculus* and *Calothyrsus* (after Hardin, 1957, 1960).

related taxa in eastern North America, eastern Asia, and southeastern Europe-Asia Minor (e.g. *Liquidambar* [Map 7], *Fagus* [Map 9], *Carpinus*, *Epigaea*) and 30 genera that have disjunct related taxa in eastern North America, western North America, and eastern Asia. At least a dozen genera (e.g. *Erythronium*, *Ostrya*, *Hepatica*, *Platanus*, *Waldsteinia* [Map 10], *Cercis*, and *Aesculus* [Map 11] occur only in all four areas, and at least six more wide-spread genera have related species distributed in this pattern. In all, at least 146 genera of eastern North America (13 per cent of the indigenous genera of seed plants) are involved; almost half of these (67 genera) are woody plants.

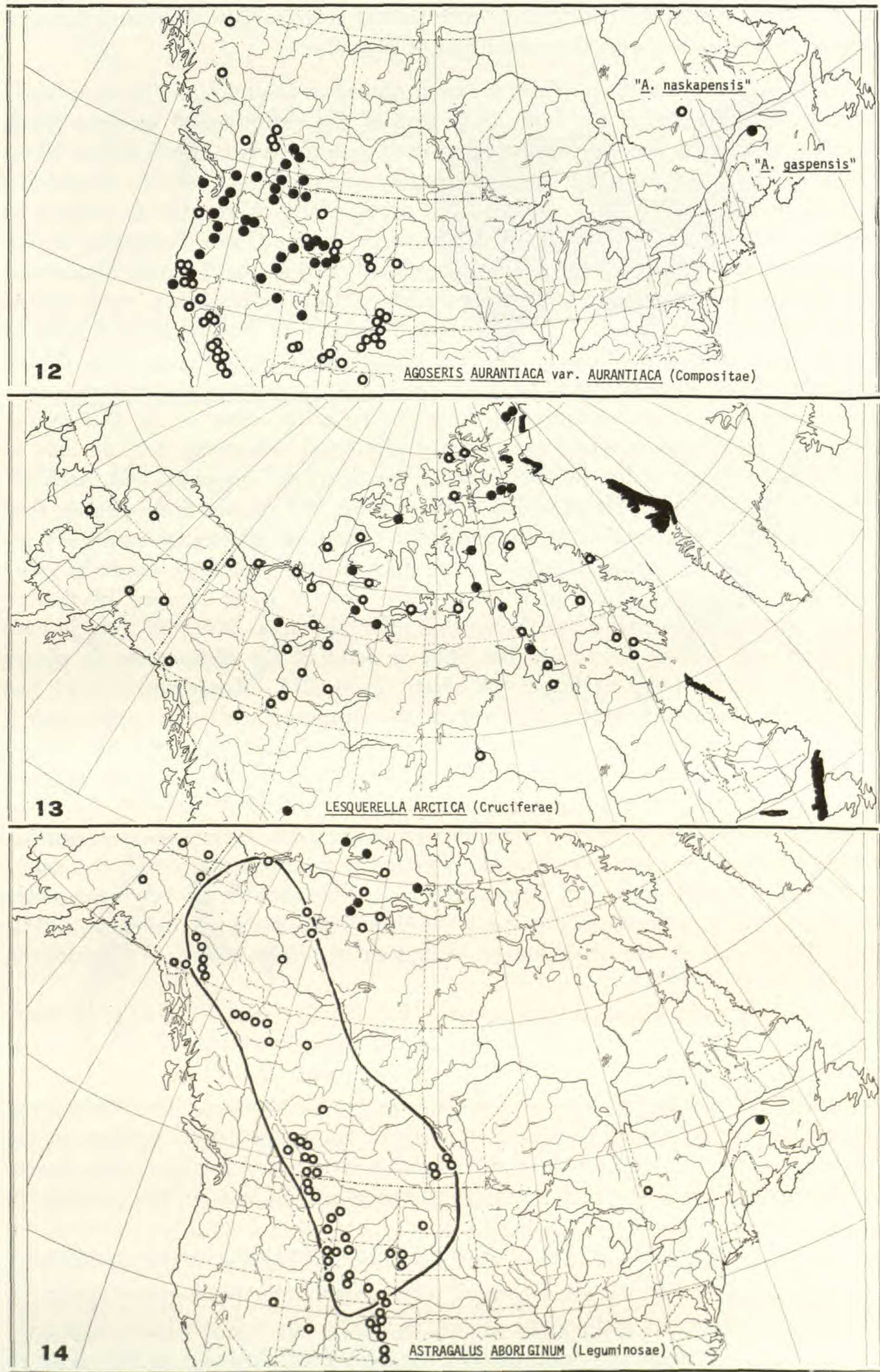
Over the years paleobotanical findings have confirmed the widespread occurrence of many of these same genera, mainly the woody ones, in Eurasia and North America in broad areas from which they are now missing, and it is clear that the extant representatives of the same widely distributed woody genera are the survivors of the gradual climatic deterioration, volcanism, orogenic movements, and the glaciations that followed.

Wolfe (1969) has pointed out that the representatives of some lineages that were present in the Tertiary in Pacific Northwestern America were able to adapt to changing climatic conditions (especially the switch from wet summer to dry summer) and now survive in different associations, others became extinct, and others survive in what are essentially relict habitats (especially in the Klamath Range of northern California and southern Oregon). The same undoubtedly was true in other regions of the Northern Hemisphere. The four disjunct areas, though, are the present more or less mesic refugia for many of the surviving descendants of formerly more widespread genera. The largest, and ecologically most complex, of the relict areas are eastern Asia and eastern North America; those of western North America and Europe-Asia Minor are smaller, and many genera that formerly occurred in them have disappeared (e.g. *Ulmus* and *Liquidambar* [Map 7] from western North America; *Tsuga* from Europe; *Liriodendron*, *Magnolia*, and *Nyssa* [Map 8] from both).

The general pattern of formerly wide boreal distributions that were fragmented by orogenic movements, gradual climatic cooling, volcanism, and the Pleistocene glaciations seems to be well established, but much is unknown. The majority of the plants involved are as yet unknown as fossils (but palynologists might well look routinely for their pollen grains, even though many are not wind pollinated). The taxonomic interrelationships in many of the genera need much more study; it is not certain that all of the disjunctions are of the same age; their areas of survival during the Pleistocene are for the most part unknown; and the accumulating

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MAPS 12-14. Western North American or arctic taxa with disjunctions in eastern North America.—12. *Agoseris aurantiaca* var. *aurantiaca*, dots, localities mapped by Fernald (1925) for *A. gaspensis* and *A. gracilens*; circles, additional collections mapped by Quentin Jones; see text.—13. *Lesquerella arctica*, black areas and dots, localities mapped by Fernald (1925); circles, additional localities mapped by Rollins and Shaw (1973); stations in northeastern Greenland and Siberia not shown.—14. *Astragalus aboriginum*, dots and outlined area as mapped by Fernald (1925); circles, localities mapped by Barneby (1964), three Alaskan stations not shown.

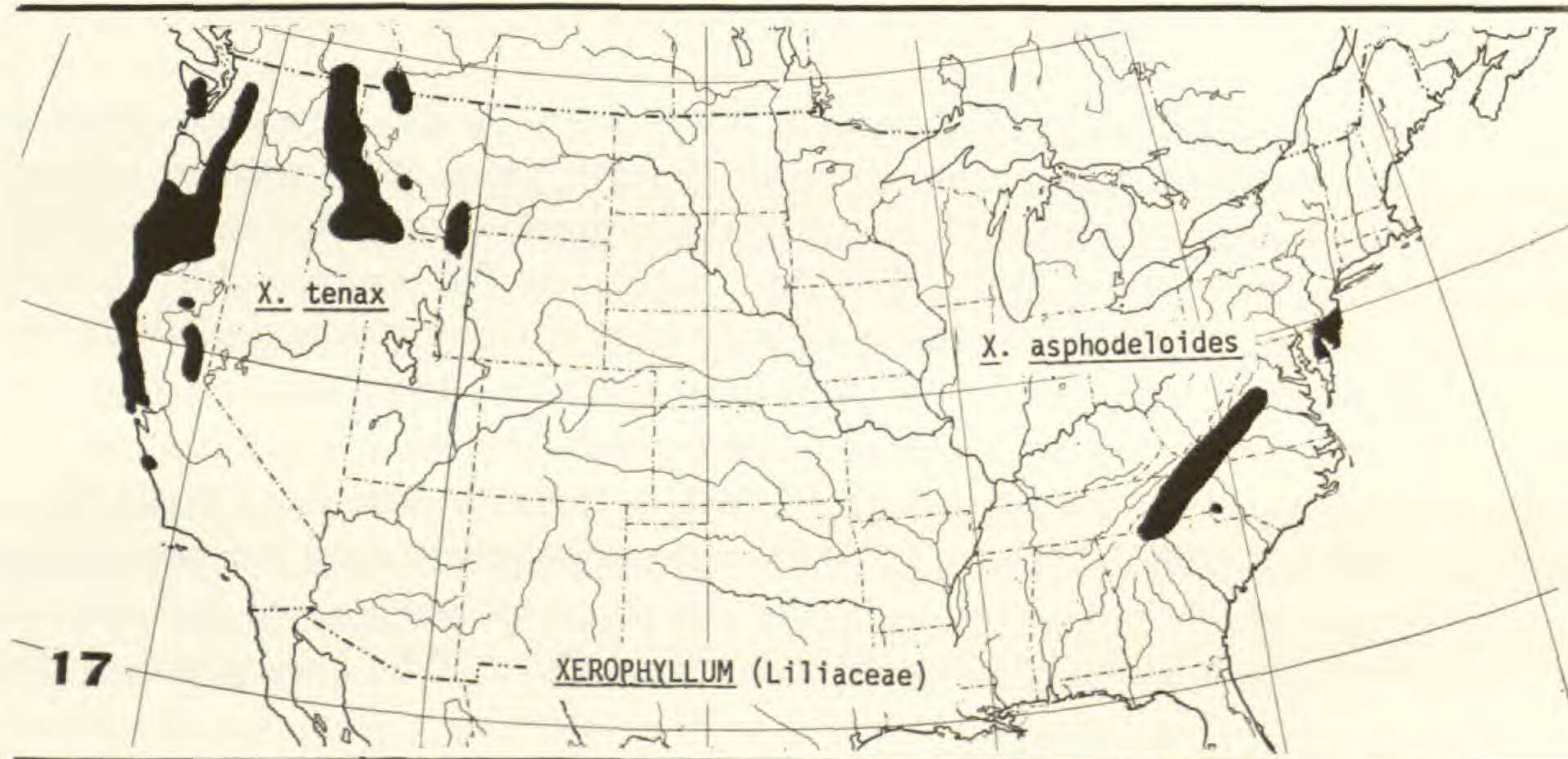
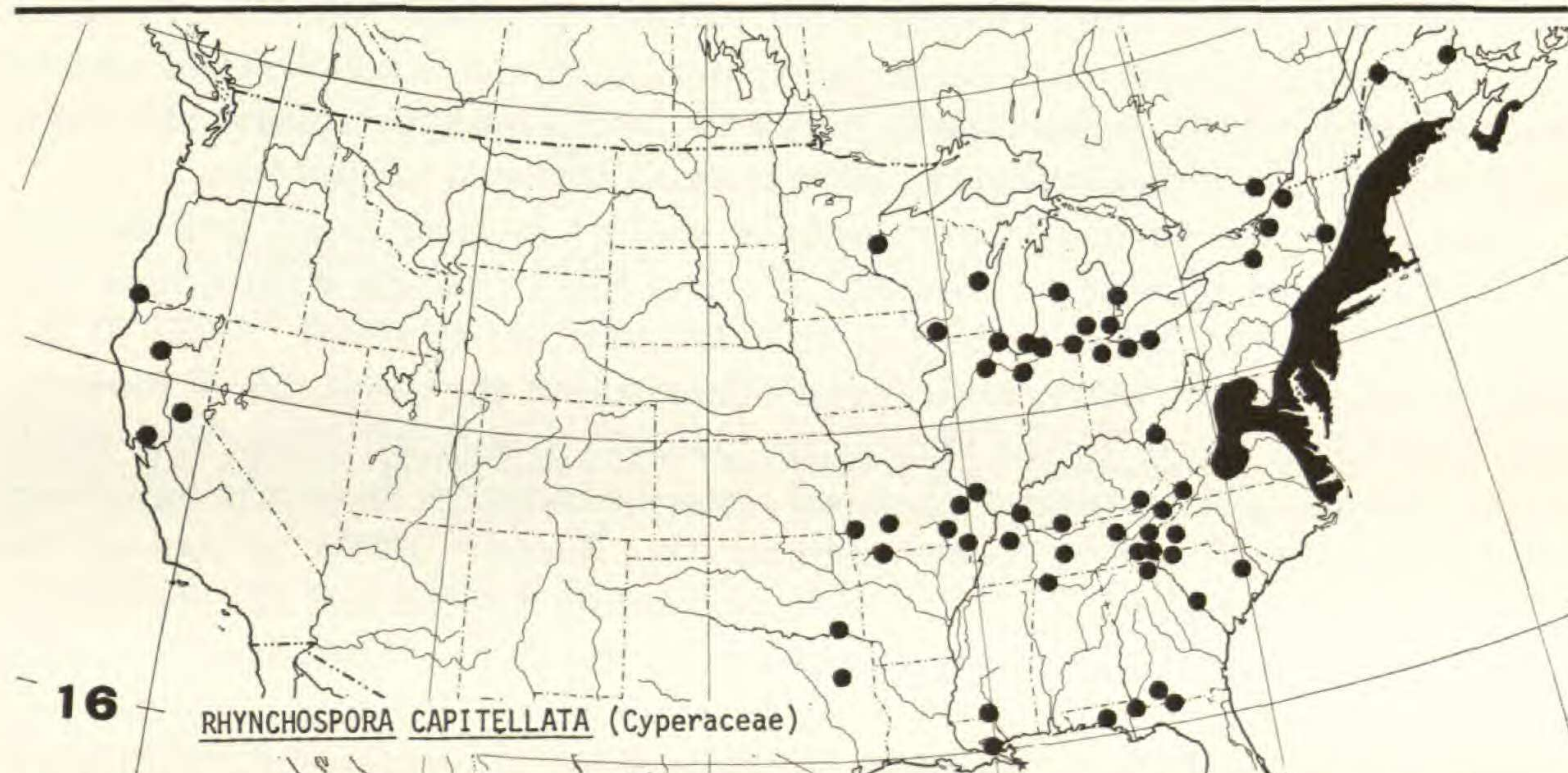
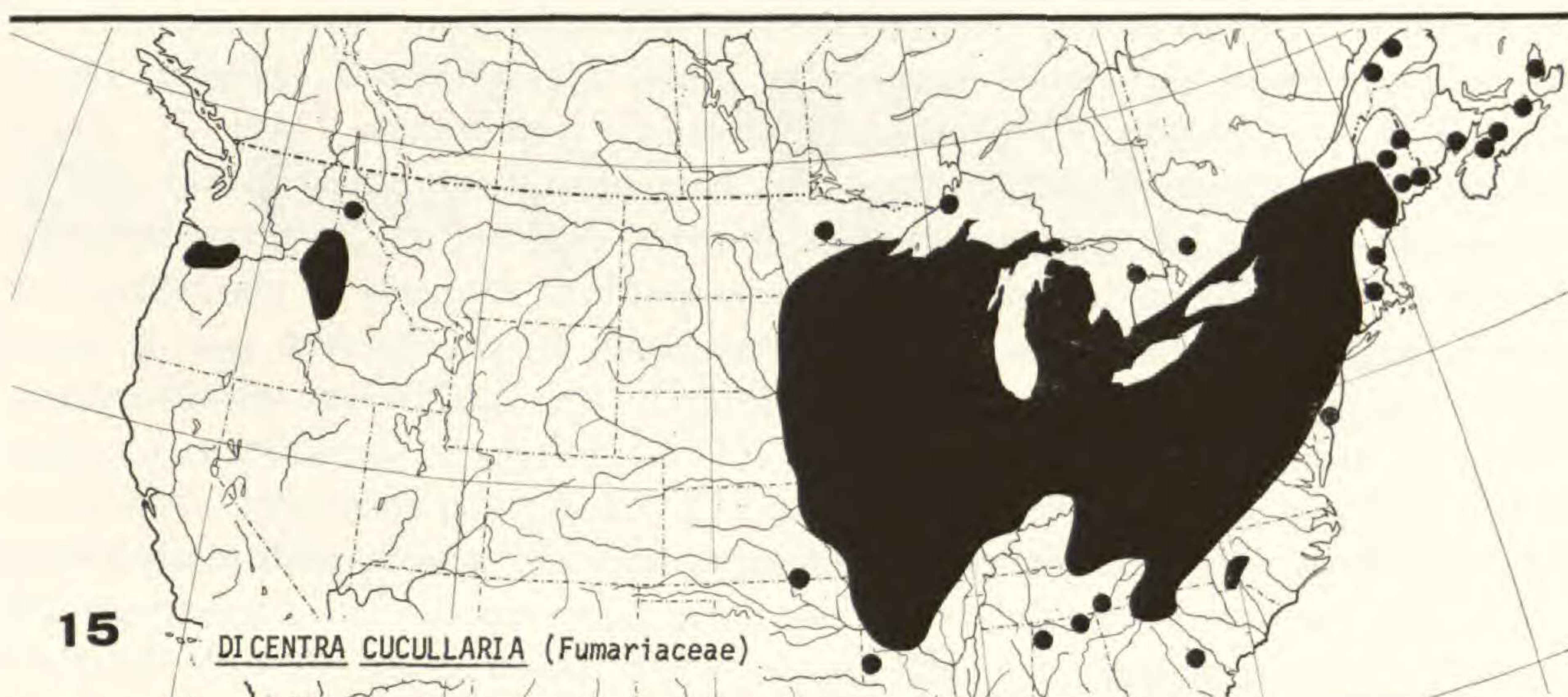


proof of continental drift introduces new spatial relationships that must be considered in connection with the migrations of plants.

Eastern North American–Western North American Disjuncts.—The now familiar pattern of species of the high arctic and of the cordillera of western North America disjunct in the glaciated area of northeastern North America (see Maps 12–14, 21) has received much attention, largely as a result of Fernald's stimulating hypothesis (1925–1935) that western and arctic plants were able to survive in unglaciated *nunatak* areas around Lake Superior, on the Gaspé Peninsula, on the tablelands of the Long Range of Newfoundland, and in the Torngat Mountains of Labrador, and that the surviving populations of these "old species" were unable to spread from these areas. "This failure of the plants of the unglaciated spots to extend their ranges into closely adjacent areas which, upon the melting of the Labrador sheet, became open territory ready for invasion, is interpreted as a further evidence of the antiquity of these plants; at the close of the Pleistocene they were already too old and conservative to pioneer, although they are able to linger as localized relics in their special undisturbed crannies and pockets" (Fernald, 1925: 243). He provided a list of some 295 species and varieties that either show this disjunction or are endemics (about 80 species or varieties) related to species of western North America and showed that these occur in areas that were thought by many geologists of the time to have escaped glaciation. However, subsequent work has shown that all of the areas involved were indeed glaciated, and further field work has filled in some of the disjunctions in places that undoubtedly were glaciated (*cf.* Maps 12, 14, 21). Monographic work has changed the taxonomic status of many of the supposed endemics, suggesting a shorter period of isolation. The work of a number of ecologists, too, has shown that the arctic plants are restricted to high altitudes or to river canyons or other places where their requirements for cold are met, and that many of the other relicts or endemics are plants of unstable habitats (cliffs, talus slopes, serpentine barrens) where they can grow but are removed from competition with the dominant eastern boreal plants (*cf.* Rune, 1954). In this last respect they apparently are similar to the endemic species of ultramafic soils studied by Kruckeberg (1951, 1967, 1969) and to the shale-barren endemics of Virginia and West Virginia studied by Platt (1951).

In reviewing the disjuncts from northwestern North America, Schofield (1969) summarizes, "The most plausible explanation of their disjunction is that the eastern representatives are remnants of a more widespread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America. The Pleistocene glaciations can be assumed to have eliminated the north-central portion of the range, but since habitats were available in north-eastern and western North America the species survived, probably south of the glacial boundary, but possibly in nunataks or coastal refuges, moving to their present sites following retreat of the ice sheet but being eliminated from their Pleistocene refugium by the encroaching vegetation and by a succession toward more mesophytic temperate vegetation. Evidence for nunataks and refugia in eastern North America has been disputed."

Much less attention has been focused on East-West disjuncts to the south of

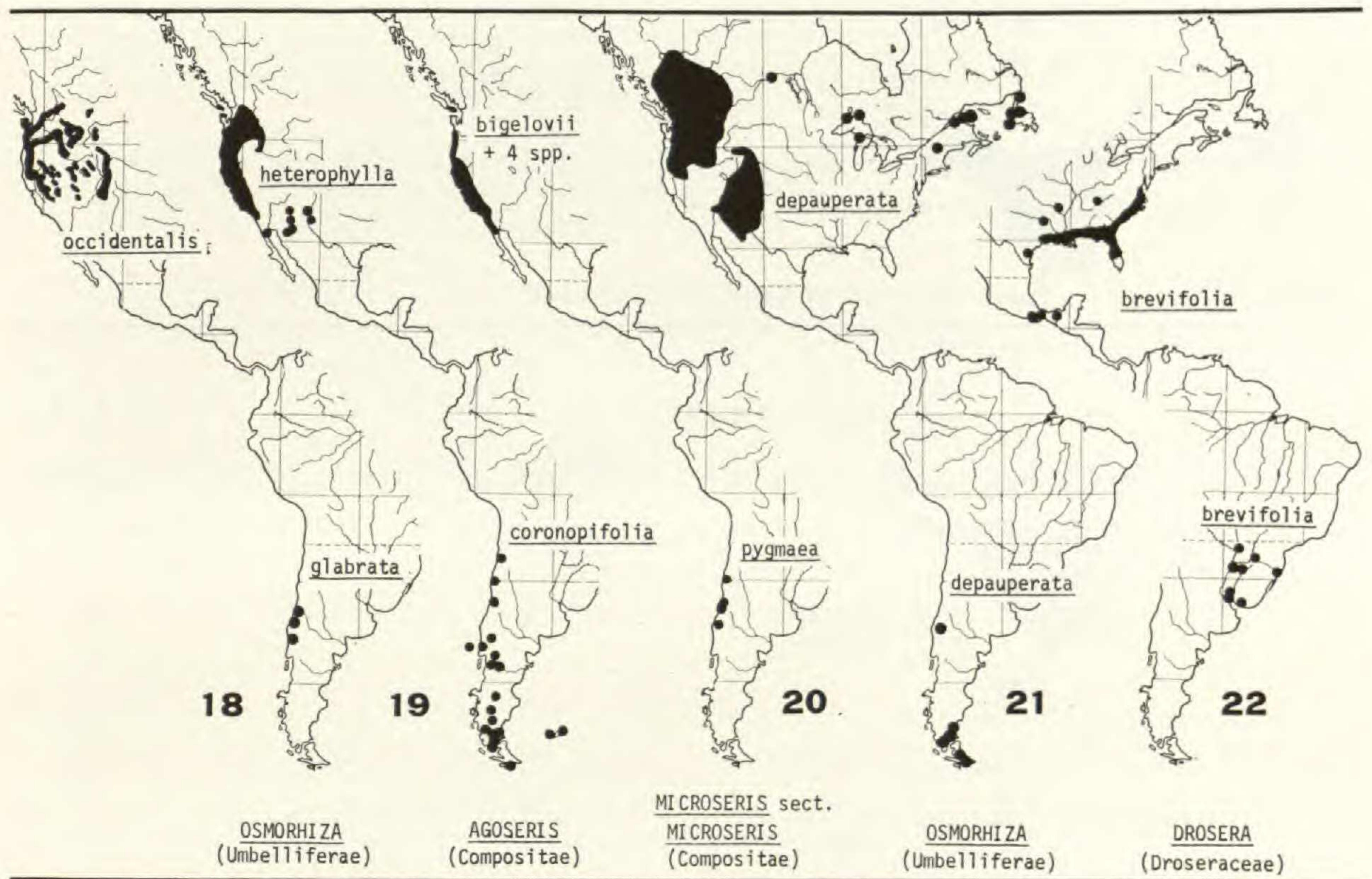


MAPS 15-17. Some taxa of unglaciated eastern North America with a disjunction to western North America.—15. *Dicentra cucullaria* (after Stern, 1961).—16. *Rhynchospora capitellata* (from Wood, 1971).—17. *Xerophyllum* (from Wood, 1971).

the maximum extent of the Pleistocene ice, although some vicarious pairs of species (*e.g.* *Pinus strobus*–*P. monticola*, *Thuja occidentalis*–*T. plicata*, *Dirca palustris*–*D. occidentalis*, *Calycanthus floridus*–*C. occidentalis* [Map 5], *Xerophyllum asphodeloides*–*X. tenax* [Map 17]) have often been cited. Wood (1971) has sorted out over 150 genera with taxa showing disjunct relationships between the part of the Appalachian mountain system south of the area of glaciation and western North America. This group includes some 50 genera with one or more species that appear to be disjunctly distributed (*e.g.* *Dulichium arundinaceum* [Map 23], *Rynchospora capitellata* [Map 16], *R. globularis*, *Ranunculus pusillus*, *Sibara virginica*, *Dicentra cucullaria* [Map 15], *Viola canadensis* vars. *canadensis* and *corymbosa*, and *Trichostema brachiatum*) and 112 genera with related taxa of the same rank on both sides of the continent. Among the latter group are 20 genera that are restricted (or nearly so) to North America and 46 with distributions that suggest the Arcto-Tertiary relict pattern (*cf.* Maps 5–6, 10). In all, at least 158 genera (14 per cent of the indigenous genera of seed plants of eastern North America) have disjunctions between the southern Appalachians and western North America either within the same taxon or between related taxa.

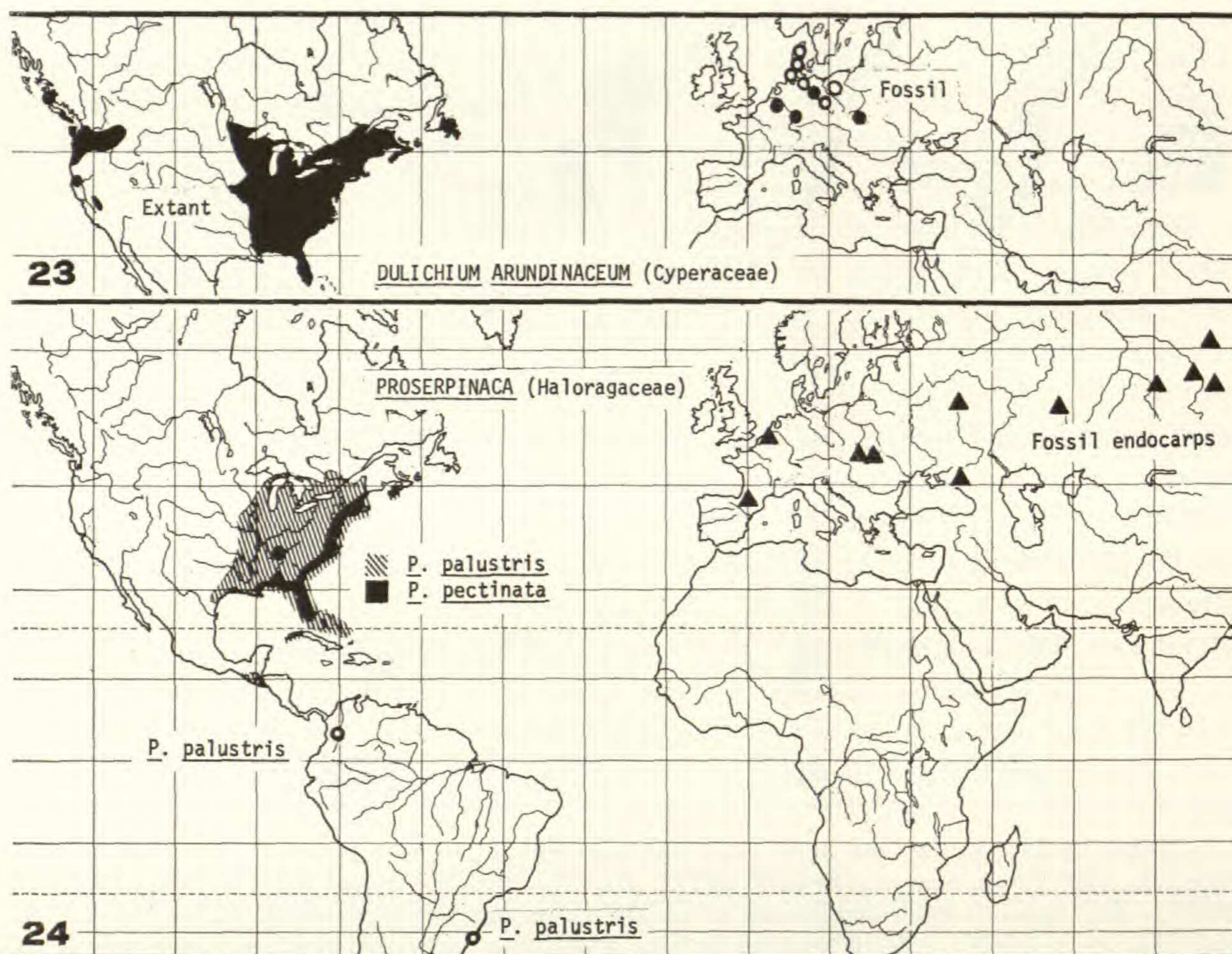
Most of the taxa involved have not been studied in great detail, and the distributional history of most is unknown. It seems likely that the disjunctions may be of different ages, since various taxonomic ranks are involved. Some fit the relict Tertiary pattern, others probably are the result of the disruption of formerly more continuous ranges by the Pleistocene glaciations, and still others may possibly be examples of long-distance dispersal. In some instances there may have been several disruptions, such as those postulated by Russell (1956) to account for the East-West disjunction of *Viola macloskeyi* subsp. *pallens* and the occurrence of both subsp. *pallens* and subsp. *macloskeyi* in the West. Whatever the causes of disruption, one of the key issues is the question of how much of a vegetational shift southward was brought about by the Pleistocene glaciations (*cf.* Whitehead, this symposium).

Amphitropical Disjunctions between North and South America.—Monographers and floristic workers over a period of many years have pointed out examples of disjunctions from both boreal and temperate North America to corresponding climatic parts of South America, mostly on the western side of both continents (Maps 18–22, 24) and disjunctions from the Sonoran and Chihuahuan desert regions of North America to deserts of northern Argentina and northern Chile. In summarizing a symposium on the amphitropical relationships in the herbaceous flora of the Pacific coast of North and South America (Quart. Rev. Biol. 38: 109–177. 1963), Raven (1963) brought together the most comprehensive catalog to date of the herbaceous examples and thoroughly discussed the possible ways in which such disjunctions could have come about. The amphitropical disjunctions fall into three groups: “bipolar or high-latitude, with about 30 species; temperate, with about 130 species; and desert, with a substantial number.” In the herbaceous plants of all three groups (the first two are entirely herbaceous), the disjunction involves either the same species or closely related subspecific taxa in both areas. In the bipolar examples, the northern taxon is also either circumboreal



MAPS 18–22. Some taxa with an amphitropical disjunction between North and South America.—18. *Osmorhiza occidentalis* and *O. glabrata*, a species-pair (after Constance & Shan, 1948).—19. *Agoseris heterophylla* and *A. coronopifolia*, another species-pair (after Jones, 1954, and Chambers, 1963).—20. *Microseris* section *Microseris*, with five species in western North America and *M. pygmaea* in South America (after Chambers, 1955, 1963).—21. *Osmorhiza depauperata* (after Constance & Shan, 1948).—22. *Drosera brevifolia* (in part after Wynne, 1944).

in distribution or (in a few cases) belongs to a circumboreal group. Of the examples of temperate disjuncts brought together by Raven, in 111 instances the North American taxon is a species of western North America, in 13 is wide-spread in North America, and in 6 is a species of eastern North America. The desert disjuncts include both woody plants (with no species common to the two areas and with few common genera) and herbaceous ones (with either the same or closely related species in both areas). Some of the amphitropical disjuncts in all three categories have been studied in considerable detail, others have been recognized from herbarium materials on purely morphological grounds. In summary, "Pertinent general considerations are that: (1) the North and South American populations are closely related; (2) the plants are almost without exception self-compatible and often autogamous; (3) they constitute an unbalanced assemblage entirely unrepresentative of the two extratropical areas; (4) they grow almost exclusively in open communities, not in woodland or scrub associations; (5) there are no corresponding cases among terrestrial vertebrates and very few among the insects; and (6) the floras of the two areas have been distinct since at least the middle Cretaceous and are still very different at present. The only explanation that accounts for all of these facts seems to be that at least the great majority of the plants reached their disjunct areas by long-distance dispersal relatively re-



MAPS 23-24. Two genera formerly distributed in the Eastern but now restricted to the Western Hemisphere.—23. *Dulichium*, the single species disjunct between east and west in North America; dots, Tertiary; circles, interglacial records (after Tralau, 1959); black, extant distribution, generalized (after Wood, 1971).—24. *Proserpinaca*, *P. palustris* disjunct in Central America, Colombia, and Brazil; *P. pectinata* disjunct in Tennessee (both after Fassett, 1953); triangles, Tertiary occurrences (after Dorofeev, 1958).

cently. For the bipolar species, the Pleistocene seems the most likely time of dispersal; for the temperate species, the late Pliocene or Pleistocene; and for the desert species, excluding those that may have differentiated from common ancestors that spanned the tropics, no time has probably been more likely than the recent past. Both bipolar and temperate disjuncts have come mostly from the north . . . and are almost entirely herbaceous. The desert disjuncts, on the other hand, often appear to have originated in the south . . . or to have diverged from a common tropical ancestor. Many of them are woody" (Raven, 1963).

Throughout all three of these examples of general patterns of distribution it is apparent how crucial taxonomic relationships and comparative morphology are in the study of disjunctions. Gray's "identical species" in eastern America and Japan have already been mentioned, as has the status of some of Fernald's Gaspé endemics that have been shown to be a part of the variation in more widespread western species. As one example of the latter, both *Agoseris gaspensis* and the later-described *A. naskapensis* (from Chicoutimi County, Quebec), along with the western *A. gracilens* (from which Fernald differentiated his *A. gaspensis*),

have been included by Quentin Jones (1954) in the western American *A. aurantiaca* var. *aurantiaca* (Map 12). Jones notes that both of the eastern disjuncts fall well within the range of variability in the polymorphic var. *aurantiaca* and that if the source of the collection were unknown it would be impossible to refer it with any assurance either to the disjunct eastern populations or to the Rocky Mountain ones. This changed taxonomy not only merges *A. gaspensis* and *A. gracilens* with *A. aurantiaca*, but includes an eastern population (*A. naskapensis*) from an area that undoubtedly was glaciated, producing a rather different problem in disjunction from that seen by Fernald (1925).

Similarly, the enlargement of *Perideridia* (Umbelliferae) by Chuang and Constance (1969) to include the Asiatic *Pterygopleurum neurophyllum* produces a different phytogeographical problem. *Perideridia* has been regarded as an entirely American genus with most of the species in the western United States and *P. americana* disjunct in the east-central United States (Map 6). However, Chuang and Constance showed that *Pterygopleurum neurophyllum*, which is distributed in southern Japan and Korea, has corky fruit ribs like those of *Perideridia howellii*, has foliage closely similar to that of *Perideridia gairdneri* subsp. *borealis*, and, most decisively, has "exactly the type of polystelic tuberous root found in most species of *Perideridia* (except *P. Howellii* and *P. Kelloggii*), a feature unknown in *Cenolophium*, *Ligusticum*, or *Sium*," the other possible genera to which it might be related. Accordingly they included the species in *Perideridia* as *P. neurophylla*. "The confirmation of the close similarity and probable affinity of this Asiatic species to the taxa of *Perideridia* inhabiting Pacific Northwest America suggests that the genus may once have been considerably more widely distributed in the northern hemisphere, perhaps before Pleistocene glaciation."

At a different taxonomic level, disjunct relationships between the species of a genus may be seen to be very different when the taxonomic framework is overhauled. The genus *Aesculus* (revised by Hardin, 1957, 1960) has an interrupted distribution in Asia, southeastern Europe, eastern North America, and western North America (Map 11). The four species of the Himalayas and China, however, belong to a different section of the genus from the geographically adjacent *A. turbinata* of Japan, which, with *A. hippocastanum*, of the Balkan Peninsula, constitutes section *Aesculus*. The Himalayan and Chinese species find their closest relative in the North American *A. californica*, the five comprising section *Calothyrsus*! The remaining American species constitute three sections (two monotypic) without disjunctions between their species.

Osmorhiza (Umbelliferae), *Amsonia* (Apocynaceae), *Gaultheria* (Ericaceae), and *Styrax* (Styracaceae) all have representatives in eastern North America, as well as in the western part of the continent. However, in each genus the species of the eastern United States belong to a different alliance from their western congeners, and, in each instance, they are morphologically closer to species of eastern Asia than to the much nearer western ones (cf. Wood, 1971: 378). In *Gaultheria*, for example, the two eastern American representatives, *G. procumbens* and *G. hispidula* var. *hispidula*, both members of section *Gaultheria*, are respectively most closely related to *G. pyroloides* (of section *Leucothoides*) and *G.*

hispidula var. *japonica*, of Japan. Of the three quite different western American species, *G. ovatifolia* and *G. humifusa* belong to section *Amblyandra*, and *G. shallon* belongs to section *Brossaeopsis*, which also includes two species of the West Indies and those of Mexico (*cf.* Shaw, 1940). Consequently, although the genus is of disjunct distribution in North America, the proper phytogeographic comparison of the eastern species is not with those in western North America but with species of Asia.

It is obvious, too, that as the state of knowledge of a flora changes, as it becomes better known, and as floras of other areas become better known, new discoveries may greatly alter phytogeographical relationships. At the time Gray (1859) wrote his important paper on the relationships between the floras of Japan and North America, he had rather scant Japanese material and little or nothing from China. Continued exploration, particularly of China and adjacent Indochina and Burma, has brought in new collections that have made possible better taxonomic decisions, and many new examples of close relationships between the floras of China and Japan and of China and eastern North America have been found. Even relatively recently, the discovery in eastern China of a white-flowered species of *Calycanthus* (described as *C. sinensis* in 1963, and raised to generic rank as *Sinocalycanthus* by Cheng and Chang, 1964) added a new morphological dimension to the genus and confirmed the relict relationship suggested by the occurrence of *Chimonanthus* (the only other genus of the family) in China and of species of *Calycanthus* in the eastern United States and in California (Map 5).

As a result of his studies of Asiatic plants Gray suggested that relatives of "monotypes" of eastern North America should be sought in Asia, and, with the continuing botanical exploration of Asia, numerous examples of this relationship have been found (*e.g.* in *Saururus*, *Decumaria*, *Itea*, *Berchemia*, and *Gordonia*, to name only a few). One of the more recently recognized instances of this relationship is that of the monotypic endemic genus *Anemonella* (Ranunculaceae). *Anemonella thalictroides*, of wide distribution in open deciduous woods over much of the eastern United States, is a low, herbaceous, tuberous-rooted plant with *Thalictrum*-like foliage and a reduced inflorescence of *Anemone*-like flowers with a perianth of five to ten conspicuous white or pinkish tepals. Although usually treated as a distinct genus, it has occasionally been referred to *Anemone*. Boivin (1957), however, prompted by comments of A. J. Eames that *Anemonella* and *Thalictrum* are the only genera of the Ranunculaceae with multiple carpellary traces, found that *Anemonella* should be referred to *Thalictrum* section *Physocarpum*. Aside from *T. clavatum*, of the southern Appalachians, and the very similar *T. mirabile*, of Kentucky and Alabama, both of which seem to be more closely related to Asian taxa than to *Anemonella*, this section is composed of twelve species of eastern Asia. The tuberous roots, the compound leaves, and the tepals, stamens, carpels, and fruits of *Anemonella* fit well with those of species of this section. A number of the species have subopposite or opposite leaves; *T. tubiferum* and *T. filamentosum* have two opposite leaves, as in *Anemonella*; and *T. coraneum* and *T. chiaonis* have reduced inflorescences. The tendencies toward

reduction in leaves and inflorescences seem only to have been carried somewhat further in *Anemonella*, and the plant fits well in *Thalictrum* (but not at all in *Anemone*, from which it differs fundamentally in leaves, inflorescences, and carpels). Accordingly, *Anemonella* became, rather redundantly, *Thalictrum thalictroides*, and a further disjunct relationship between eastern North America and eastern Asia became evident.

Discoveries that alter the distributional patterns that led Fernald to think in terms of nunataks have already been mentioned, and a few of these are seen in the maps of *Agoseris aurantiaca*, *Lesquerella arctica*, and *Astragalus aboriginum* (Maps 12–14). In another geographic direction, work on the flora of the State of Santa Catarina, Brazil, has added species such as *Arenaria groenlandica*, *Xyris brevifolia*, *Hypericum gentianoides*, and *Proserpinaca palustris* (Map 24) to the list of plants that are disjunct in Brazil from the main body of their distribution in the eastern United States (*cf.* Raven, 1963); and other examples of this disjunction have been found.

Beyond these considerations, one of the principal problems in understanding disjunctions is our meager knowledge of the past distributions, the expansions and contractions in the ranges, of most plants. The fragmentary palaeobotanical record will always leave much to be desired, and the usefulness of palaeobotanical data is further impaired by misidentifications made by uncritical workers. Many of these misidentifications are based upon fossil leaves that it may or may not be possible to identify on the basis of detailed studies, and many of the reports based on fossils of this type must be discounted, at least for the present. The comments of Tralau (1963: 40) in his review of Eurasian fossils attributable to *Magnolia kobus* are pertinent: "It is, nevertheless, uncertain and can not be decided here whether all these finds [of leaves] really belong to the genus *Magnolia* or not. On the other hand fossil foliar specimens referred to the genera *Juglans*, *Ficus*, *Anona*, *Persea*, *Lindera*, *Laurus*, *Eriobotrya*, *Evodia*, *Rhododendron*, *Ardisia*, *Solandra*, and possibly even others actually may be remains belonging to *Magnolia*. Because of this obvious uncertainty the prospect of unravelling the problems associated with these remains and reconstructing the Tertiary history of *M. Kobus* with them is most unattractive."

Some groups, however, have been reviewed carefully and now have relatively well-documented fossil records based on wood, fruits, and pollen (*e.g.* *Nyssa*, Map 8, after Eyde & Barghoorn, 1963; *Fagus*, Map 9, after Tralau, 1962) that show that the present disjunctions are the remnants of formerly broad ranges. Fossil pollen, in particular, is proving to be helpful in showing the presence of various genera of flowering plants in areas where they no longer occur (*e.g.* the well-documented pollen record of *Liquidambar* in Eurasia, and the growing pollen record of *Pachysandra* in western North America).

Contrary to the assertions of many plant geographers, present distributions do not necessarily indicate where a group of plants has occurred in the past, although there are exceptions. On the basis of similarities in the modern distributions of plants that are restricted in their occurrence to the four areas where Tertiary relicts occur it can be inferred that genera such as *Narthecium*, *Erythro-*

nium, *Asarum*, *Aesculus*, and *Waldsteinia* (see Maps 10–11) were formerly distributed around the Northern Hemisphere as *Nyssa* and *Fagus* were. However, the modern distributions of most plants may not show where they have occurred in the past, and many speculations about origins, migrations, and disjunctions can be nothing more than speculations unless other evidence can be found.

For example, the sedge *Dulichium arundinaceum* is widely distributed in the eastern United States and occurs quite disjunctly in the Pacific Northwest and in a few localities in California. One cannot suspect from its extant range that it formerly occurred in western Europe, where fossil remains of it are known from a number of localities (*cf.* Map 23, after Tralau, 1959). Further, in the aquatic genus *Proserpinaca* (Haloragaceae), *P. pectinata* is mostly confined to the Coastal Plain of the southeastern United States, while the other species of the genus, *P. palustris*, is more widely distributed in eastern North America and has disjunct occurrences in Central America, Colombia, and southern Brazil (Map 24). Certainly there is nothing in this distribution to suggest that *Proserpinaca* formerly occurred in Europe and Asia, but Dorofeev (1958) has illustrated fossil endocarps that he assigns to two species analogous to the living ones. Although on the basis of morphology of the all too similar endocarps, the recognition of two extinct species hardly seems justified, these endocarps certainly represent *Proserpinaca* and document a formerly wide Eurasian range for the genus. These two examples, to which many others can be added, show that distributions of individual species have changed in the past—and undoubtedly are still changing—and strongly suggest that in dealing with disjunctions the phytogeographer must be wary of interpretations based only on extant distributions.

Morphology, then, is basic to the taxonomy of both extant and extinct plants, and, consequently, to the study of disjunctions. As in taxonomy, however, there are questions that cannot be answered by morphology alone, and evidence from other disciplines must be sought. For most species of living plants it is unlikely that we shall ever have any sort of fossil record that will show where their ancestors grew, but detailed studies involving morphology coupled with ecology, cytology, genetics, physiology, and other disciplines will undoubtedly provide many clues that will be of great importance in explaining the many patterns of disjunction. Some data will provide answers, some will only be suggestive, and some will raise still further questions. The other papers in this symposium show some of the varied ways of approaching these problems, but in all of them morphology, the foundation of taxonomy and plant geography, is always the cornerstone, no matter how elaborate the structure it supports.

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